# CLIFF-NESTING ADAPTATIONS OF THE GALÁPAGOS SWALLOW-TAILED GULL[1]

JACK P. HAILMAN

E. CULLEN (1957) showed that the cliff-nesting Black-legged Kittiwake (*Larus* (*Rissa*) *tridactylus*) differs from "typical" (i.e., ground-nesting) gulls in many respects. The species' unique morphological and behavioral characters. Cullen cogently argued, have resulted from adaptation (either directly or indirectly) to cliff-breeding. Epistemologically, the correlation between cliff-nesting and unusual characters constitutes a hypothesis that must be "tested" independently on a relatively unrelated cliff-nesting gull. Therefore, while I was studying the chick-feeding behavior of the cliff-nesting Galápagos Swallow-tailed Gull (*Larus* (*Creagrus*) *furcatus*) I noted the general habits of this species for comparison with the Kittiwake.

## METHODS

The results of observations of the colony on southern Plazas Island off Santa Cruz (Indefatigable) Island and of several colonies on Tower Island. made during November, 1962, are presented in tabular form with explanatory comments in the text. The observations are compared with characteristics of the Kittiwake and "typical" ground-nesting gulls.

The horizontal distance from the outer edge of the nest to the edge of the nesting ledge was measured with a tape measure in the beginning, and later estimated by eye; the vertical height of the nest above the sea was estimated by eye. Behavioral observations were made with binoculars and in some cases recorded photographically with still and motion pictures. Notes on the nocturnal habits. breeding cycle, and displays of *furcatus* are presented elsewhere (Hailman, 1964*c*, 1964*a*, and in prep., respectively).

In this and other publications on gulls I have followed the latest family revision (Moynihan, 1959), which assigns all species of gulls to the genus *Larus*. Except where noted, all information on the Kittiwake's adaptations has been taken from Cullen (1957). Information for comparisons with "typical. ground-nesting gulls" has come primarily from Cullen (1957), my unpublished notes on *Larus atricilla*, Tinbergen (1953), and accounts in Bent (1921).

In the "visual cliff" experiment reported below, a standard, albeit makeshift. visual cliff apparatus (Fig. 3) was made from a wooden box 16.5 inches long. 11 inches wide, and 9 inches deep. Across the glass top ran a center

[1] To Ernst Mayr (on the occasion of his 60th birthday), who taught me that the study of whole animals is not only an intellectually respectable pursuit but moreover an exciting life's devotion.

strip of black tape (3.5 inches wide) upon which the chick stood. To one side of the strip was the plain glass ("deep" side), under which the inside of the box lined with square-ruled paper (0.9 mm squares) could be seen. On the other ("shallow") side, ruled paper lined the underside of the glass. Each chick was placed in the center of the strip under a small translucent box for a 30-second habituation period, after which the box was lifted and timing with a stop-watch begun. Ten newly hatched *furcatus* chicks raised from the egg in a dark incubator were tested. The chick was scored as having chosen a side (i.e., deep or shallow) if it placed one foot on that side so that the foot did not touch the center strip. If no choice was made within 10 minutes, the chick was scored as "no choice" and was gently pushed toward the deep side or pinched in order to force a choice.

## CLIFF-NESTING OF THE SWALLOW-TAILED GULL

*The actual cliff habitat.*—There are certain important differences between the "cliff" habitat of the Swallow-tailed Gull and the Kittiwakes. (1) The Swallow-tail nests on lava ledges or barancas whose angle varies from vertical to nearly horizontal, while the Kittiwake nests almost exclusively on vertical cliffs. (2) The two gulls nest at different heights, the Kittiwake sometimes very high (130 meters), the Swallow-tail at variable heights (1 to 25 meters), rarely higher than 8 meters (Fig. 1). (3) The Kittiwake's cliff almost always overlooks the sea, while that of the Swallow-tailed Gull may overlook land near the water (e.g., the colony in NW corner of Darwin Bay on Tower Island). (4) Similarly, flat land at the top or foot of the nesting cliff, or at least near it, is available to Swallow-tails for display activities; this is usually not so true for Kittiwakes. (5) Finally, the distance from the nest to the edge of the cliff gives some idea of the restriction of living space and of the likelihood of eggs or chicks falling off the cliff. Minimum distances from the center of the nest to the edge are shown in Figure 1 for a sample of 41 nests of the colony at Plazas. Apparently all Kittiwakes nest on ledges which just barely hold a nest and two standing adults, so each nest is placed at about the shortest distance found for the Swallow-tailed Gull (25–50 cm). (Recently, however, Kittiwakes have begun nesting on flat ground; see Paludan, 1955; Coulson, 1963).

*Possible selective pressures producing cliff-nesting habits.*—Cullen (1957) believes that the Kittiwake's cliff-nesting is an adaptation to avoid predation on the eggs and chicks, and even upon the adults. Predation is probably unimportant in the Swallow-tailed Gull (see below), since its nest predators would be primarily aerial (and thus would have access to the nest) no matter where the gulls nested in the Galapagos (Hailman, 1964*c*). However, even aerial predators, such as Frigatebirds (*Fregata* spp.) may have difficulty

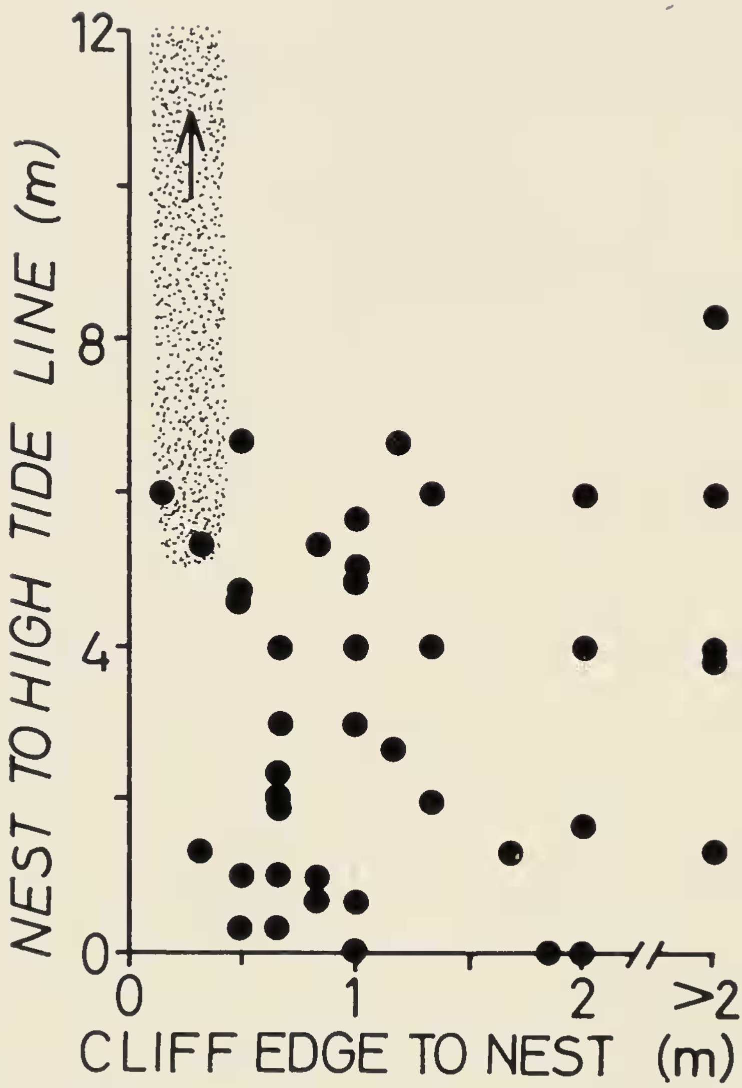


FIG. 1. Sites of 41 active nests of *Larus furcatus* on South Plazas Island, November 1962. The median height is 4 meters above the sea. The stippled portion indicates nest sites of *Larus tridactylus*, which go to above 130 meters, with median values of 15–35 meters above the sea (Coulson, 1963).

landing on narrow ledges; aerial predators also have difficulty landing on the Kittiwake's ledges. The Swallow-tailed Gull's cliff-nesting might be linked in some way with pelagic habits; such an idea, if correct, would probably also apply to the Kittiwake. Also, the *furcatus* population may merely have exploited an unoccupied niche. The number of "typical" nesting sites for gulls (high grass in sand dunes or marshy area) is severely restricted in the Galápagos. which may account for the small population of the endemic Lava Gull (*L. fuliginosus*), a "typical species." (Food may also limit *fuliginosus* due to competition with other species for refuse; Hailman, 1963.)

ENVIRONMENTAL CONDITIONS AND CORRELATED CHARACTERISTICS

*"Selective pressures" accompanying cliff-nesting.*—The multiple differences from typical gulls shown by the Kittiwake are presumably the results of sev-

eral separate selective pressures. Probably only some of these selective pressures act on *furcatus*, partly because of the habitat differences (above). Thus, if Cullen's hypothesis be correct, the relatively unrelated Swallow-tailed Gull should prove convergent with the Kittiwake in those characters presumably related to situations that both species experience; in other respects the Swallow-tail should resemble typical gulls.

Specifically, the special environmental conditions experienced by the Kittiwake as a result of its cliff-nesting habits are: (1) reduced room for nesting; (2) scarcity of nesting sites; (3) scarcity of nest materials; (4) relaxation of predation on nest and eggs; and (5) danger of eggs rolling off cliff and chicks falling off cliff. (I have altered this classification somewhat from Cullen's presentation.)

(*1*) *Reduced room for nesting.*—The nesting space of individual pairs of cliff-nesting birds is limited to small ledges, particularly if all possible nest-sites are utilized by the species. To hold as large a territory around its nest as does a ground-nesting gull, the ancestral cliff-nesting gull would have had to defend many separate ledges. Deviant individuals psychologically "satisfied" with defending merely the nesting ledge might have left more offspring because parental care improved with lessening of territorial disputes (see discussion of "aggressive neglect" in Hutchinson and MacArthur, 1959). The converse holds for ground-nesters, which gain an anti-predator advantage by spacing-out.

Some problems arising from this reduced living-space are: (a) reduced space for territorial "fighting" and display; (b) reduced room for display and copulation between mates; (c) undue hostility aroused between mates because of continual propinquity; and (d) fouling of the nest. Some adaptations to these problems are summarized in Table 1, and further explained by the following notes.

In the early part of the nesting season, Kittiwakes display on the water at the foot of the cliff (Tinbergen, 1958). That Swallow-tailed Gulls do not appear to do this might be explained by the fact that they have available other areas for display (see above). Twice I observed copulation on flat land near the nesting-cliffs but never saw it on the cliffs (which were watched for much longer periods of time). E. Curio (pers. comm.) also observed copulation once on the flat surface of a large rock. Allo-preening within the pair (J. M. Cullen, 1962) is probably a "display" evolved to reduce hostility. (This characteristic was not commented upon by E. Cullen, 1957, but was discovered in the cliff-nesting tern *Anous tenuirostris* by J. M. Cullen and Ashmole: see Postscript to this paper.)

Appeasement Head-flagging exhibited between Kittiwake chicks is absent

TABLE 1

CHARACTERISTICS PRESUMABLY RELATED TO AMOUNT OF NESTING SPACE

| SPECIES | TYPICAL GULLS | SWALLOW-TAILED GULL | KITTIWAKE |
|---|---|---|---|
| Living Space: | Large | Reduced | Small |
| 1. *Fighting* | | | |
| a. frequency | frequent | infrequent (?) | frequent |
| 2. *Displays* | | | |
| *a. chasing and moving displays | several | none (?) | a few |
| *b. long distance displays | several | none (?) | a few |
| *c. upright threat | common | absent (?) | absent |
| d. Long Call ceremony | loud | silent (?) | "Kittiwaking" (?) |
| *e. pairing displays | on pairing territory | occasionally on flat land | occasionally at base of cliff (and top of) |
| 3. *Copulation* | | | |
| *a. where | on ground | on ground | on ledge |
| *b. female | stands | stands | sits on tarsi |
| 4. *Hostility Reduction* | | | |
| *a. allo-preening (pairs) | absent (?) | present | present |
| *b. Head-flagging (adults) | uncommon | uncommon (?) | common (in certain situations) |
| *c. Head-flagging (chicks) | absent | (never seen) | present |
| *d. dark neck band | absent | immatures | chicks |
| 5. *Prevention of Fouling* | | | |
| a. older chick defecates (cf. Table 4:2e) | off nest | over ledge | off nest or over ledge |
| b. eggshells (cf. Table 4:1d) | parents remove or eat | parents remove | not removed |

* See Table 6.

in *furcatus*, which has only one chick per clutch. (I saw Head-flagging, or something like it, only twice in adult birds.) I do not know whether or not strange Swallow-tail adults landing on a nest tend to peck the chick; in this situation the Kittiwake chick Head-flags. The very dark neck band of *tridactylus* chicks used in appeasement ("Bill hiding"—Cullen, 1957: Figure 1) is likewise absent in *furcatus* chicks. However, such a neck band is found in white-plumaged (prefledged) immature birds, which interact with their parents and possibly birds on other territories. (This band is shown in Hailman, 1964*c*: Figure 2.)

(2) *Scarcity of nesting sites.*—The Swallow-tailed Gull may breed at any time of the year (Hailman, 1964*a*; Leveque, 1964:87), although Snow (Hatch, pers. comm.) has found recent evidence that individual pairs breed on a 10-month cycle. Furthermore, synchrony of breeding is pronounced only in local areas, not on whole islands or between islands (Hailman, 1964*a*), although Snow's recent observations and also those of E. Curio indicate a general

TABLE 2

CHARACTERISTICS PRESUMABLY RELATED TO AVAILABILITY OF NESTING SITES

| SPECIES: | TYPICAL GULLS | SWALLOW-TAILED | KITTIWAKE |
|---|---|---|---|
| Nesting Sites: | Abundant | Ample (?) | Scarce |
| *1. Reduction of Competition* | | | |
| a. breeding | seasonal | probably a 10-month cycle, with islands not in phase | seasonal |
| b. site | stereotyped | varied | stereotyped |
| *2. Territory* | | | |
| *a. when assumed | after pairing | probably after pairing | before pairing |
| b. guarding before first egg laid (cf. Table 3:3b) | rare | sometimes | always, but not necessarily continuously |

* See Table 6.

synchrony within whole colonies as well (Curio, pers. comm.). Therefore the competition for nesting sites might be less acute than in the seasonally breeding Kittiwake. Furthermore, on Tower Island I noticed many unused areas that seemed to me capable of supporting *furcatus* nests. However, this situation seems to be true of Kittiwakes as well. The real competition for nest sites may be for nest sites *near other pairs.* Probably as a result of a reduced competition for nest sites, the territory of the ledge is not guarded (at night) before the egg is laid as strongly as after this time. Adaptations to nesting space are summarized in Table 2.

(3) *Scarcity of nest materials.*—Kittiwakes compete for nesting material because vegetation does not grow on the breeding cliffs. For such materials, the birds must go to flatter land, which they "fear" (Cullen, 1957). The Swallow-tailed Gull solves the vegetation shortage by using lava stones (Fig. 2), and sometimes coral fragments and sea urchin spines, all of which I found abundantly near the nests in which they occurred. This difference in abundance of materials correlates well with the multiple differences between the two species (Table 3).

There is some local synchrony of the general breeding cycle among *furcatus* pairs within sight and sound of one another. However, this synchrony may be an "accidental" extension of the normal responses to displays of the mate (i.e., a sort of "behavioral pleiotropism") and may not have been specifically selected for (Hailman, 1964*a*). The Swallow-tailed Gull's synchrony is certainly not as remarkable as the specific synchrony of building found in Kittiwakes. The latter's unique building synchrony was thought to be due to the availability of mud only on rainy days and to the social process of inland collecting (Cullen, 1957).

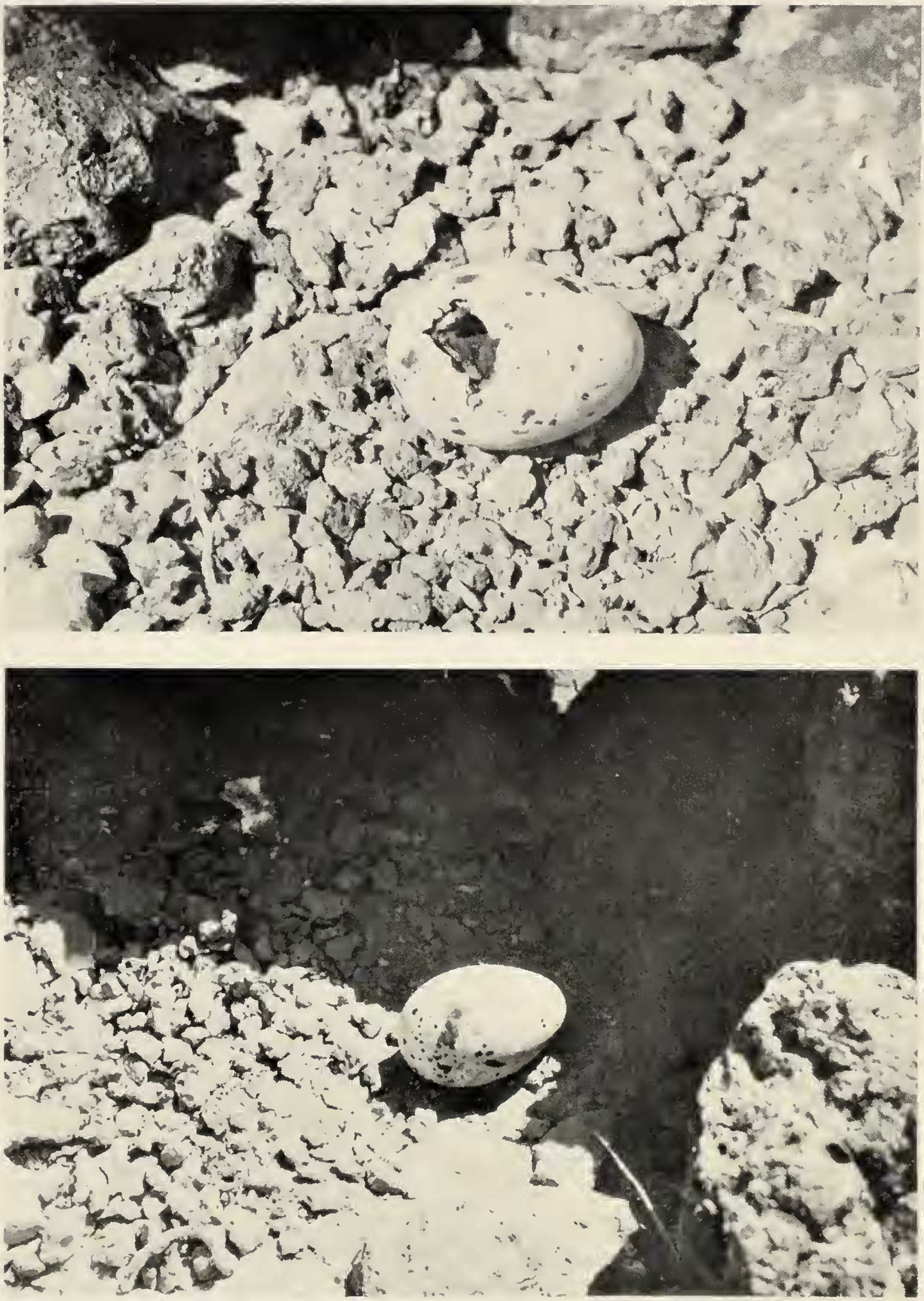

Fig. 2. Nests of *Larus furcatus*. a. (above) a typical nest of lava stones. The white egg tooth on the chick's bill is visible in the pipped hole. b. (below) A less structured nest placed under overhanging rocks, presumably for protection from the hot sun. In some areas, nests contain sea urchin spines and shells, as well as lava stones.

TABLE 3

CHARACTERISTICS PRESUMABLY RELATED TO AVAILABILITY OF NESTING MATERIALS

| SPECIES: | TYPICAL GULLS | SWALLOW-TAILED | KITTIWAKE |
|---|---|---|---|
| Materials: | Abound | Abound | Scarce |
| 1. *Nest Materials* | | | |
| a. materials used | vegetation | lava stones | mud and vegetation |
| *b. place | near nest | near nest | distant areas |
| *c. collecting | individual | individual | social |
| 2. *Building Nest* | | | |
| *a. timing | individual | individual | synchronized |
| *b. technique | simple | simple | elaborate |
| 3. *Stealing from Other Nests* | | | |
| *a. frequency | seldom | seldom | often |
| b. guarding before first egg laid (cf. Table 2:2b) | rare | sometimes | always |

* See Table 6.

(4) *Predation at the nest.*—In Kittiwakes, nest predation (e.g., by foxes) is virtually eliminated because of the inaccessibility of the nest. However, in the Galapagos there are relatively few potential predators that cannot fly (e.g., two species of native rats which, however, climb readily) so the cliff-nesting habit of *furcatus* has not completely eliminated nest predation. Frigatebirds (*Fregata magnificens* and *F. minor*), which abound in the Galapagos, regularly patrol the nesting-cliffs. Furthermore, the native owl *Asio galapagoensis*

TABLE 4

CHARACTERISTICS PRESUMABLY RELATED TO AMOUNT OF NEST PREDATION

| SPECIES: | TYPICAL GULLS | SWALLOW-TAILED | KITTIWAKE |
|---|---|---|---|
| Nest predators: | Aerial and ground | Aerial | (none) |
| 1. *Parental Protection* | | | |
| *a. alarm call | frequent | frequent | rare |
| *b. flight distance | far | variable (far to very near) | near |
| *c. attacks | vigorous | variable (vigorous to very weak) | very weak |
| d. eggshells (cf. Table 1:5b) | parents remove or eat | parents remove or eat | not dispersed |
| 2. *Eggs and Chicks* | | | |
| a. egg coloration | cryptic | cryptic | cryptic |
| b. clutch size (cf. Table 5:2a) | three | one | two |
| *c. plumage | cryptic brown | cryptic gray | not cryptic |
| *d. behavior | hides in vegetation | hides in cracks | does not hide |

* See Table 6.

TABLE 5

CHARACTERISTICS PRESUMABLY RELATED TO DANGER OF FALLING OFF CLIFF

| SPECIES: | TYPICAL GULLS | SWALLOW-TAILED | KITTIWAKE |
|---|---|---|---|
| Cliff danger: | (none) | some | great |
| *1. Eggs and Chicks* | | | |
| a. clutch (cf. Table 4:2b) | three | one | two |
| *b. nest | shallow cup of vegetation | shallow cup of stones | deep cup of vegetation |
| *2. Chicks* | | | |
| *a. stay in nest | a few days | long period | long period |
| *b. face toward | any direction | cliff wall | cliff wall |
| *c. locomotion | frequent | immobile | immobile |
| *d. when attacked | run | do not run | do not run |
| *e. flight movements | vigorous | intermediate | weak |
| f. "visual cliff" behavior | random choice (?) | avoid deep side | ? |
| *g. feed from | ground and parent's bill | parent's bill | parent's throat |
| *h. parental feeding call | present | present | absent |

* See Table 6.

(which hunts both by day and night) and the hawk *Buteo galapagoensis* probably prey on *furcatus* nests (Murphy, 1936). In fact, one of the primary selective advantages of nocturnal habits of *furcatus* may be to allow the parents to stand guard at the nest through all the daylight hours when the aerial predators abound (see Hailman, 1964*c* for a discussion of other possible factors). However, it is not known whether the parent's merely being at the nest actually reduces predation or not.

Table 4 compares anti-predator adaptations in typical gulls, in *furcatus* and in *tridactylus*. Reduction of the clutch size might make a nest less conspicuous to predators, thereby decreasing the probability of destruction of all the eggs (also see below). However, this possible reduction of predation would not seem, a priori, to be of such magnitude to offset the approximately 66 per cent reduction in productivity caused by fewer eggs. Table 4 indicates that not only *furcatus* (Fig. 2) but also *tridactylus* have cryptically colored eggs. Cullen (1957) considers this crypticity to be ancestral, and, although of no benefit to the Kittiwake, retained because it is of no disadvantage.

(5) *Danger of falling off the cliff*.—Most Kittiwakes nest at the very edge of a real precipice; Swallow-tailed Gulls do not, on the average, nest in such a dangerous situation, although certain individuals may (see Fig. 1). Kittiwakes prevent eggs from rolling out of the nest by making an extra deep nest cup, whereas Swallow-tails use lava stones (Fig. 2). I tried rolling eggs out of several *furcatus* nests and found it very difficult (much more so than from

the nest of *L. atricilla*, the American Laughing Gull, for instance). Gulls themselves might accidentally dislodge the egg from the nest, though possibly other natural causes do too. Curio (pers. comm.) recorded one incidence of sea breakers washing an egg from its nest. Possibly the reduction of crowding due to the small clutch size also helps prevent eggs from rolling over the ledge.

One trait not appearing in Table 5 requires comment. Cullen (1957:300) notes that the Kittiwake has "strongly developed claws and toe-musculature" compared with ground-nesting gulls. The Swallow-tailed Gull appeared to me to have strong claws as well, but no stronger than those of the Lava Gull, *L. fuliginosus*. I attributed this similarity to the fact that the latter species, although not a cliff-nester, spends its life on the rock substrate of Galapagos shores. However, I later compared a long series of specimens at the U. S. National Museum, and could find no consistent differences between species of gulls, adults or chicks. Perhaps important differences are obscured in dried skins, so further checking of claws and musculature in the field is desirable.

Emlen (pers. comm.) is attempting to do "visual-cliff" experiments (Walk and Gibson, 1961) on the Kittiwake. Emlen (1963) has already shown that newly hatched chicks of the ground-nesting Herring Gull (*L. argentatus*) may avoid the deep side of an artificial "cliff." However, his apparatus and experimental procedures are sufficiently different from the standard visual-cliff situation that a direct comparison with the usual experiments cannot be made. Cullen (1957) reports that chicks of the ground-nesting Black-headed Gull (*L. ridibundus*) placed in *tridactylus* nests wandered "blindly" off the cliff. However, Shinkman (1963) showed that newly hatched domestic chicks (*Gallus gallus*) do recognize and avoid the deep side of a visual cliff apparatus; this shows that such perceptual organization is possible in a newly hatched precocial bird.

Of the ten newly hatched chicks I tested, six chose the shallow side, one the deep, and three made no choice during the 10-minute test period. The probability that this choice is due to chance is small (binomial of $\frac{1}{7}$ is $p = 0.062$). Of the three immobile chicks, one turned and stepped onto the shallow side when pushed toward the deep; the other two refused to take a step in any direction. It is further of interest that the single "deep-choosing" chick scampered ("without looking") onto the deep side immediately upon removal of the translucent box. Thus, it seems quite likely that *furcatus* chicks (like those of *Gallus gallus*) possess depth perception at hatching.

Cullen (1957) considers that the feeding of Kittiwake chicks is adaptive to cliff-nesting. Most gull species (including *furcatus*) regurgitate food upon the ground or hold it in the bill in response to the chick's pecking at red markings on the parental bill. (The marking is a white tip in *furcatus*, presumably an adaptation to nocturnal feeding: Hailman 1964*b*, 1964*c*.) However, Kittiwake chicks take food from the throat of the parent. Lacking red markings on the bill, the parent Kittiwake has a bright red throat, to which the chicks direct pecking-like movements when it is open (although they also peck at the yellow beak; J. M. Cullen, pers. comm.). It could be that the releaser has been moved inside the bill so that Kittiwake chicks will not be tempted to approach adults and topple over the edge of the cliff. At any rate, chicks do not need a "long distance signal" in order to find the parent, nor does the parent require a Pumping display of the chick in order to find its offspring (Cullen, 1957). Since the Swallow-tailed Gull's feeding is additionally influenced by its nocturnal timing, it is not reasonable to expect this species' throat to become white, since this would probably reflect very little light indeed. However, the *furcatus* parent does have a "feeding call" that releases the approach of the chick, as has *atricilla* (Hailman, 1964*b*) and other ground-nesting species. The Kittiwake lacks this call, presumably to prevent accidentally calling chicks over the cliff.

Since in all other adaptations relating to prevention of falling over the cliff, *furcatus* resembles *tridactylus* (see Table 5), the chick-feeding differences seem to be anomalous. I suggest that in all species bill and throat colors are also under selective pressures relating to displays between adults. I have argued elsewhere, for instance, that the position of the white bill-tip of *furcatus* in relation to the white feathers at the base of the bill indicates the displaying bird's head position in very low light intensities (Hailman, 1964*c*). Surely the throat color of all gull species is evident during displays in which the mouth is held wide open during vocalizations. It is possible, then, that the chick-feeding method is influenced by display-methods and vice versa.

## DISCUSSION AND CONCLUSIONS

*Multiple selective pressures.*—Few characteristics are governed by only one selective pressure during evolution. Thus, the removal or eating of eggshells and the young chick's droppings might serve both to prevent fouling of the nest and to prevent discovery of the nest by predators. Tinbergen and co-workers (1962) have demonstrated by field experiments that nests with broken eggshells are found and destroyed by predators more readily than nests without shells. Fouling has not been studied experimentally. Older chicks of all species defecate out of the nest. However, Kittiwakes with little nest predation defecate on the nesting ledge, while Swallow-tailed Gulls with more predation defecate over the ledge. This difference suggests that predation is important as a selective agent in defecation habits. Also, guard-

TABLE 6

SUMMARY OF THE SWALLOW-TAILED GULL'S MORPHOLOGICAL AND BEHAVIORAL CHARACTERISTICS

| Environmental conditions | Morphological/Behavioral Characteristics* Like ground-nesting Gull species | | Intermediate | | Like or equivalent to Kittiwakes | |
|---|---|---|---|---|---|---|
| *Like Kittiwake* | | | | | | |
| reduced nesting space | 4 | 6 | 0 | 1 | 6 | 11 |
| cliff danger | 2 | | 1 | | 5 | |
| *Intermediate* | | | | | | |
| nest sites scarce | 1 | 5 | 0 | 2 | 0 | 0 |
| nest predation | 4 | | 2 | | 0 | |
| *Like Ground-Nesters* | | | | | | |
| nest materials scarce | 5 | | 0 | | 0 | |

* Those relatively unambiguous characters marked with an asterisk (*) in Tables 1–5. See text.

ing of the nesting ledge prior to laying may serve to protect both the site and the nesting materials from being usurped by conspecifics in Kittiwakes (see above).

The clutch size of *furcatus* might be explained by Lack's (1954) proposal that clutch size in birds is determined by the number of young that can be fed successfully, although there seem to be other factors acting as well. The essence of Cullen's (1957:289 ff) interpretation of the reduction of clutch size from three to two in the Kittiwake seems to be a special case of Lack's hypothesis: if a pair of gulls can feed only two young successfully, Kittiwakes need lay only two eggs to have the maximum clutch, while "typical" gulls must lay three since there is a high probability that at least one will die from causes other than starvation (e.g., predation) that do not affect Kittiwake chicks.

Cullen's suggestion probably could not apply to the Swallow-tailed Gull, which has many potential nest predators. Instead, two additional hypotheses were advanced for *furcatus* (above). The first, that clutch reduction makes the nest less conspicuous to predators, is presumably not effective in Kittiwakes because of the lack of predation. However, I think it is unlikely as the major force in reducing clutch size in *furcatus*. The other explanation, lessening of crowding of eggs and chicks to prevent their accidental falling over the cliff, might operate in Kittiwakes as well, although Cullen does not specify this possibility.

However, still a fourth factor may be acting in the Swallow-tailed Gull, one that is a corollary of Lack's hypothesis. The breeding period of seasonally breeding gulls coincides with the abundance of food available for the young and clutch size is expanded to utilize the food maximally. In tropical species for which food is available in moderate supply the year around, the long nocturnal trek at sea for food may severely restrict the number of chicks that can be fed successfully. Although laying but one egg, *furcatus* pairs may actually rear more than one chick per year by breeding more often than annually (Snow's recent evidence, mentioned above, indicates a 10-month cycle).

*Test of Cullen's hypothesis.*—With the data at hand, we are now in a position to test E. Cullen's (1957) hypothesis that the peculiarities shown by Kittiwakes are indirectly the result of selective pressures accompanying cliff-nesting habits. Given the degree of environmental similarity in Kittiwakes and Swallowtails, we can see how closely their characters match. (The following comparison omits (a) characters that cannot be evaluated as being either like Kittiwakes or ground-nesting gulls and (b) characters that cannot be assigned, a priori, to a single presumed selective pressure.)

Table 6 divides 30 characters of *L. furcatus* into a matrix of the degree of similarity with *tridactylus* versus the degree of similarity of the environmental conditions presumably related to the characters. It is evident that in those respects in which the environmental conditions (i.e., presumed selective pressures) are similar, the morphological and behavioral characters are also similar. Taken as a whole, the data constitute a clear vindication of Cullen's (1957) hypothesis that peculiarities of the Kittiwake are the result of special selective pressures that accompany cliff-nesting.

Why does the Swallow-tailed Gull in some respects resemble ground-nesting gulls when the environmental characteristics are similar to those of Kittiwakes? Several answers are possible. (a) First, *furcatus* does not experience as extreme an environment as does *tridactylus*, even in those respects where the environment is designated as "like Kittiwake" in Table 6. (For instance, Figure 1 shows that the danger of falling over the cliff is not as great.) (b) Secondly, the independent adaptation of *furcatus* to cliff-dwelling may not yet have proceeded far enough to evolve the full complement of characters possessed by *tridactylus*. That is, in evolutionary time *furcatus* may be a more recent cliff-nesting species; or *furcatus* may have some kind of genetical limitations which have not produced the variation for natural selection to work upon. (c) Lastly, other selective pressures which have escaped the notice of Cullen and me might be acting upon these characters in different ways in the two species. Very probably all of these reasons have some validity. The important thing is, I think, that *furcatus* completely lacks Kittiwake-like traits where its environment resembles that of ground-nesting gulls.

*Epistemological status of comparative data concerning natural selection.*—

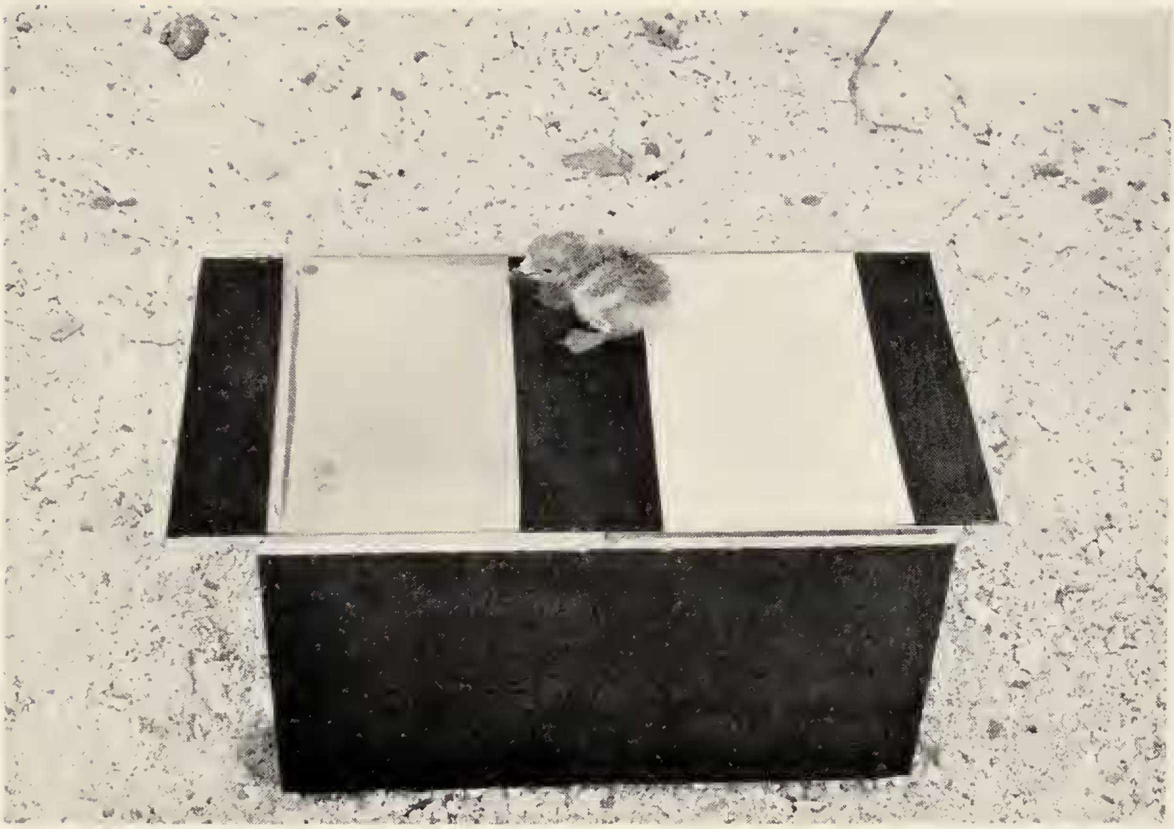

FIG. 3. A one-day-old chick of *Larus furcatus* on the visual-cliff apparatus. The chick is facing the "deep side" of the cliff. The ruled squares on the paper lining the deep and shallow sides do not show well in the photograph partly because the film used is less sensitive to blue than is the eye.

The most satisfactory method of demonstrating that a morphological or behavioral character is under the influence of a specific selective pressure is to measure that pressure within a population of organisms; deviants from the norm of the character should be more strongly selected against. For instance, Kruuk (1964) has shown that the farther a pair of Black-headed Gulls (*Larus ridibundus*) nests from the center of a colony, the heavier the nest predation by foxes.

Another method, setting up an artificial situation closely resembling the natural one, is often necessary because of the rarity of natural deviants or the difficulty of measuring deviants and differential selection in natural populations. Thus, Tinbergen et al. (1962) have shown that Black-headed Gull nests artificially set up and placed near a nesting colony will be preyed upon by both aerial and ground predators. Aerial predators find and destroy such nests more readily when broken shells are placed in or near a nest with chicks or eggs. This demonstrates rather satisfactorily at least one of the selection pressures that maintain the eggshell removal behavior of nesting adults.

Least cogent among methods of demonstrating selective pressures on specific characters is the method of this paper. A population (which may be a species. as in this case) is discovered which shows differences in morphology or behavior from other, presumably genetically related, populations. This discovery, in and of itself, is not a valid demonstration that the characters are under selective pressures due to observed environmental differences between the populations. However, this correlation does function as a *prediction* as to what characters will be found in another population with the same environment as either the deviant or the "normal" populations already known. This third population, for which the prediction was made, constitutes a valid test of the hypothesis (i.e., environment–character causation) *only* if its characters were unknown at the time of conception of the hypothesis. (Conversely. if the new population's characters were known—say from museum skins—but its environment was not, prediction of the conditions of its environment would constitute a valid method of approach.)

This indirect, "comparative" method is, however, full of methodological pitfalls. The gene pools of all populations concerned must be similar enough that the same variations would be produced for natural selection to act upon. The populations should have been isolated and living in their present environments for sufficient time for natural selection to work. Furthermore, multiple selective pressures will usually be involved, as well as selective pressures of which the investigator is unaware. There are certainly other problems as well.

In conclusion, the present method for studying natural selection has a rather low reliability. It is, however, a vast improvement over glibly assigning a "selective advantage" to a particular morphological or behavioral character just because to do so seems "reasonable" a priori.

*A Postscript.*—Shortly after the manuscript of this paper was finished, there appeared a study of the cliff-nesting tern, *Anous tenuirostris* (the Black Noddy). J. M. Cullen and N. P. Ashmole (1963) found many differences between this species and other terns, and these unique characters closely resemble those of the Kittiwake and the Swallow-tailed Gull. The one "new" possible cliff-nesting adaptation reported for *furcatus* (allo-preening), Cullen and Ashmole discovered in the Black Noddy as well. Their study adds a further confirmation of E. Cullen's (1957) hypothesis.

## SUMMARY

The Galápagos Swallow-tailed Gull (*Larus* (*Creagrus*) *furcatus*) nests on shallow to steep cliffs. In some respects (i.e., reduced nesting space, danger of falling over cliff) its environmental conditions resemble those of the cliff-nesting Kittiwake (*L.* (*Rissa*) *tridactylus*). Unlike *tridactylus*, *furcatus* has abundant nesting materials available, as do ground-nesting gulls such as *L. argentatus* and *atricilla*. In some aspects of its ecology

(availability of nest sites, amount of nest predation) *furcatus* is intermediate between the *tridactylus* and ground-nesting gulls.

Many behavioral and morphological characteristics of *furcatus* were noted in field study and experiments. Thirty of these are unambiguous enough for comparison with the other species. Of those characters presumably adaptive to the environmental conditions shared with ground-nesting gulls, all five resembled the characters of the ground-nesting species. Of seven characters presumably related to the "intermediate" ecological conditions, five resembled characters of ground-nesters and two were intermediate. Finally, of 17 characters presumably adaptive to conditions shared with the Kittiwake, 11 resembled those of the Kittiwake, one was intermediate, and 6 resembled those of ground-nesting species.

Thus, Cullen's (1957) hypothesis that the Kittiwake's unusual characters are adaptive to special ecological conditions accompanying cliff-nesting is, in general, confirmed.

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DEPARTMENT OF ZOOLOGY, DUKE UNIVERSITY, DURHAM, NORTH CAROLINA (PRESENT ADDRESS: INSTITUTE OF ANIMAL BEHAVIOR, 31 FULTON STREET, NEWARK, NEW JERSEY), 11 FEBRUARY 1965